ISSN 0704-3716

Canadian Translation of Fisheries and Aquatic Sciences

No. 5448

Morphology and mode of life of Bythotrephes longimanus Leydig

G. Ischreyt

Original title: Ueber korperbau und lebensweise des Bythotrephes longimanus Leydig. (Chapters 12-17)

In: Arch. Hydrobiol. 21: 241-242 and 303-324, 1930

Original language: German

Available from:
Canada Institute for Scientific and Technical Information
National Research Council
Ottawa, Ontario, Canada K1A 0S2

1989

39 typescript pages

Secretary of State / Secrétariat d'État

90-00629/

MULTILINGUAL SERVICES DIVISION – DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU BUREAU DES TRADUCTIONS

LIBRARY IDENTIFICATION – FICHE SIGNALÉTIQUE

Translated from - Traduction de	Into - En
German	English

Author - Auteur

Ischreyt, Gottfried

Title in English or French – Titre anglais ou français

Morphology and Mode of Life of Bythotrephes longimanus Leydig

Title in foreign language (Transliterate foreign characters)
Titre en langue étrangère (Transcrire en caractères romains)

Ueber Körperbau und Lebensweise des Bythotrephes longimanus Leydig

Reference in foreign language (Name of book or publication) in full, transliterate foreign characters.
Référence en langue étrangère (Nom du livre ou publication), au complet, transcrire en caractères romains.

Archiv für Hydrobiologie

Reference in English or French – Référence en anglais ou français

Archives of Hydrobiology

Publisher - Éditeur	DATE OF PUBLICATION / DATE DE PUBLICATION			Page Numbers in original / Numéros des pages dans l'original
	Year / Année	Volume	Issue No. / Numéro	241-242 & 303-324
Place of Publication / Lieu de publication		XXI		Number of typed pages / Nombre de pages dactylographiées: 37

Requesting Department / Ministère-Client: DFO

Translation Bureau No. / Notre dossier nº: 2292525

Branch or Division / Direction ou Division: GLLFAS, Fish. Hab. Studies

Translator (Initials) / Traducteur (Initiales): IJ

Person requesting / Demandé par: Heather Cameron/Dr. Ora Johannsson

MAY - 4 1989

Your Number / Votre dossier nº:

TRANSLATION NOT EDITED FOR PUBLICATION
TRADUCTION NON DESTINEE A LA PUBLICATION

Date of Request / Date de la demande: 88/12/21

Canada

SEC 5-111 (84-10)

Secretary of State | Secrétariat d'État

MULTILINGUAL SERVICES DIVISION – DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU | BUREAU DES TRADUCTIONS

Client's No.–N° du client	Department – Ministère	Division/Branch – Division/Direction	City – Ville
	Department of Fisheries and Oceans	Fish. Hab. Studies	Burlington, ON
Bureau No.–N° du bureau	**Language – Langue**	**Translator (Initials) – Traducteur (Initiales)**	
2292525	German	IJ	MAY – 4 1989

Morphology and Mode of Life of Bythotrephes longimanus Leydig

By Gottfried Ischreyt, Libau

With 20 Figures and 24 Tables in the text

When Bythotrephes longimanus LEYDIG was discovered in Courland in (p.241) the summer of 1925 (Lake Usmaiten) and in the summer of 1926 (Lake Wehsit and Lake Saucken), this find provided the stimulus for closer study of its morphology and ecology. To my knowledge, these were the very first finds of specimens of this crustacean in the eastern Baltic region. The first public mention concerning these finds occurred during the 1204th meeting of the Association of Natural Scientists [Naturforscher-Verein] at Riga on 17 January 1927. From a paper by KUPTSCH (14) "Die Cladoceren der Umgegend von Riga" ["The Cladocera found in the region around Riga"] contained in Vol.18, No.2 of the Archives of Hydrobiology [Archiv für Hydrobiologie] issued on 21 October 1927 I gathered that Bythotrephes longimanus also occurred in Lake Lihlast near Riga and was caught there by KUPTSCH on 8 August 1924. In August 1927 I captured the crustacean once more in Lake Usmaiten and also in Lake Pussen and on 10 August 1928 in Lake Duhnje near Riga, which is interconnected with Lake Lihlast.

I was able to place my research on the subject on a broader base when Prof. THIENEMANN put his catches made in Holstein at my disposal and when I

Canada

TRANSLATION NOT EDITED FOR PUBLICATION
TRADUCTION NON DESTINEE A LA PUBLICATION

received more material from other regions, in part with his kind help. Plankton from Lake Saadjärv near Dorpat[1)] was sent to me by Prof. RIIKOJA, and Dr. OTTERSTRÖM sent me plankton from Lake Fure on the island of Zealand. Dr. EKMAN let me have a precious specimen from his catch made in Lapland. With the kind help of Dr. FREIDENFELT I received from S. ERIKSON a considerable number of specimens of Bythotrephes from Lake Värmeln in southern Sweden, while a sample of plankton from Lake Constance was sent by Prof. SCHMALZ with the help of Prof. AUERBACH. Dr. DECKSBACH sent a sizeable number of Bythotrephes taken from Lake Senesch near Moscow, and Dr. PERFILIEV provided Bythotrephes from Lake Gab in Karelia. In the two latter cases the crusta- (p.242 ceans involved were unfortunately Bythotrephes cederströmii SCHRÖDER rather than longimanus, and they therefore could not be considered for this paper.

I regret that I have been unable to complete my material any further. I did not have access to the rich plankton collection of the Hydrobiological Institute in Riga, for example, and the one catch from Lake Constance was all I could obtain from the Alpine region.

I would like to thank all those who have shown interest in my work in many ways, particularly Prof. THIENEMANN.

---

1) Translator's note: Dorpat is now called Tartu

TABLE OF CONTENTS

12. The distribution of Bythotrephes longimanus 4

13. The relationship between Baltic Bythotrephes and Nordic Bythotrephes 11

14. The colonization of Central Europe 21

15. The systematics of Bythotrephes longimanus 24

16. Some closing remarks 33

17. Bibliography 35

12. The distribution of Bythotrephes longimanus (p.303)

With the present state of our knowledge, it is not yet possible to say anything conclusive about the distribution of Bythotrephes long., either from a geographical or from an ecological standpoint.

As my own investigation proves, great care has to be taken not to exclude definitely any body of water as a possible habitat of the crustacean. There is no doubt that the distribution of Bythotrephes is more extensive than previously thought. Occasional collecting activity around lakes that have not previously been investigated might lead to positive results, but negative results on the other hand can only be taken as proof under very specific conditions.

In order to achieve a correct evaluation of the situation, large amounts of plankton have to be collected and scrutinized; otherwise any finds will be simply accidental. Furthermore, the plankton should, if possible, come from as many different sections of a lake as possible, since we know very little about the distribution of the crustacean in a horizontal and vertical direction and about its migrations. The nets used for fishing for plankton must act as efficient filters in order to obtain sizeable quantities. I believe I can refute the suggestion that Bythotrephes is too good and active a swimmer to be caught in a close-meshed net, because I caught one in Lake Pussen using a net with a mesh size of 0.07 mm. However, these circumstances are important when determining quantities.

In my experience Bythotrephes is encountered in a very wide range of bodies of water. KEILHACK and RÜHE (12) were the first to cast doubt on the belief that it occurred only in large and deep lakes. When I first started

collecting Bythotrephes I concentrated too much on the surface layers of the water and did not put enough emphasis on large amounts of plankton. Therefore my early results do not possess the same value as evidence as do my results obtained later when I had adjusted my methods of catching specimens of Bythotrephes.

Proof that Bythotrephes longimanus occurs in the eastern Baltic region fills a gap that existed between the distribution areas in Sweden, the High North and Russia. Further south the lakes of Latgale[1)], so far (p.304) unexplored in this respect, may form the transition to the find spots in Poland and North Germany.

The countries surrounding the Baltic, namely southern Sweden, Denmark, North Germany and the Baltic states in the east, form an integral geographic area which can be compared with the sub-Alpine region and the region of the High North. Why this comparison is justified will be discussed below.

Nothing conclusive can be said concerning the question of the ecological conditions of existence of Bythotrephes in the eastern Baltic region; this is due to the gaps in our knowledge of the nature of our lakes and because a close link exists between the study of lake types and of ecological conditions. The lakes around Riga have been explored in some detail for their physical and chemical properties by LUDWIG (16), but as far as the others are concerned, I have only my notes to go on which I made during short visits. The soundings I took are not always reliable either, as they often had to be taken when the water was agitated.

[1)] Note added during proof-reading: According to a letter by teacher KUPTSCH Bythotrephes have been found this summer in several lakes in Latgale.

The 20 lakes and large ponds which I encountered for the first time in Courland and the adjoining region of Livonia during the last few years are distributed in a manner which is explained below. In common language use some bodies of water have been called "lakes" although they do not have a profundal zone. Even if in such cases the term "pond" might be correct, it goes against the grain to call an open body of water anything but a lake, if it has a diameter of several kilometres, shows relatively little plant growth and strong wave activity.

In the following list those bodies of water that contain Bythotrephes are printed in spaced type; the maximum depth of a lake, if it is known to me, is put in brackets, in metres, after each name.

1. Lowland plain of Riga-Mitau: 1. Lake Stint (4.12), 2. Lake Großer Weißer [See] (6.7), 3. Lake D u h n j e - "Lake L i h l a s t" (6.4)[1]. 4. "Lake" Dsirne (4.75), 5. "Lake" Langsting (8.0), 6. "Lake" Silber (10.4).

2. Coastal plain of northern Courland: 7. Lake U s m a i t e n (approx. 15), 8. Lake P u s s e n (approx. 35 ?). (p.305)

3. Coastal plain of western Courland: 9. Libau lagoon (1-2), 10. "Lake" Tosmar (less than 1).

4. Watershed of western Courland: 11. Lake Durben (3.5).

5. Watershed of northern Courland: 12. Lake Walgum (22.5), pond near Spahren (5-6), 14. pond south of Spahren (5), 15. pond south of Spahren (7-8), 16. "Lake" Gulben west of Spahren (?).

6. Hill region of central Courland: 7. Lake Zezern (24), 18. "Lake" of Alt-Schwarden (5).

---

[1] Dr. von Transche informed me that the level of the lake is now much lower than previously due to a breach in a dyke.

7. Hill region of upper Courland: 19. Lake S a u c k e n (8.5), 20. Lake W e h s i t (23).

Thus Bythotrephes has been found in only 5 of the 20 lakes and ponds I visited.

The lakes in which Bythotrephes occurs will be dealt with first according to their depths.

As is well known, Bythotrephes was initially considered to inhabit only deep, large lakes. Then ZACHARIAS discovered that it occurred in Lake Labenz, which is 17 m deep, and RÜHE found it in Lake Zagnania (West Prussia), which is 14 m deep. These discoveries encouraged KEILHACK and RÜHE (12) to search for the crustacean systematically in a large number of lakes. They succeeded in adding 6 new find spots in the lake district of the upper Havel with an additional find in Lake Müggel made by Prof. SCHIEMENZ. The average maximum depth of 33 lakes in North Germany, which had up to then been known to be inhabited by Bythotrephes was calculated by KEILHACK and RÜHE as 33.70 m; they then compared this result with the corresponding average for the 8 new find spots, which was 14.81 m. While Lake Labenz (17 m maximum depth) had previously been considered the most shallow of the lakes in North Germany in which Bythotrephes was known to exist, it now turned out that Lake Müggel (8 m deep) and Lake Haus (only 5 m deep) were also inhabited by the crustacean. HEILHACK und RÜHE write: "We regard it therefore as likely that the hypothesis according to which Bythotrephes prefers large, deep lakes in North Germany is false and that further search for this interesting form will succeed in proving that it exists in an additional large number of smaller, shallower bodies of water in North Germany." I should point out at this juncture that (since

KEILHACK and RÜHE drew up their list) the following North German lakes have been discovered to contain Bythotrephes: Lake Dieck (THIENEMANN), Lake Höft (UTERMÖHL) and Lake Soldin (THIENEMANN).

My observations can be taken as giving general support to the views of KEILHACK and RÜHE. If I divide the bodies of water I visited into three groups according to their depths - those whose maximum depth is up to 10 m, those whose maximum depth is up to 20 m and those whose maximum depth is more than 20 m - I arrive at the result that two of the lakes containing Bythotrephes (Lake Duhnje-Lihlast and Lake Saucken) belong to the first group, one lake (Lake Usmaiten) belongs to the second and two lakes (Lake Wehsit and Lake Pussen) belong to the third group. However, the maximum depth of Lake Duhnje-Lihlast is less than 6.4 m with an average of 3.41 m. (p.306)

Since, as we have seen, no particular depth of water is necessary for Bythotrephes to exist, we cannot presume that it depends on a particularly low water temperature either. On 6 August 1906 at 5:30 p.m. LUDWIG (16) measured the temperature of Lake Duhnje-Lihlast as 19.5° C (while the temperature of the air was 16° C), and on 7 and 8 August 1924 KUPTSCH (14) measured 21.5° C at the surface of the lake and 20.8° C at a depth of 4m (while the temperature of the air was 20° C and 16.5° C respectively). Neither does Bythotrephes seem to favour the deeper parts of Lake Usmaiten in the summer, because if was precisely in the very shallow northern bay that I collected a considerable number of it on 13 August .

Another question concerns the possible dependence of Bythotrephes on a particularly high oxygen content. LUDWIG has measured the oxygen content of the upper layers of water in the lakes around Riga in the summer and found a value of 5.7 ccm per litre in Lake Duhnje-Lihlast. As this is an

isolated finding and nothing is known about the other lakes involved in this investigation, the question concerning the oxygen requirement of Bythotrephes has to remain unanswered. It can, however, be assumed that it is able to exist in water rich in O_2 as well as in water low in O_2, since it thrives in both a shallow and a muddy lake, such as Lake Duhnje-Lihlast, and in the Coregon Lakes (Usmaiten and Pussen).

At this point I would like to insert a short characterization of our bodies of water containing Bythotrephes, as far as this is possible using the observations made to date.

1. "Lake" Duhnje-Lihlast (according to LUDWIG). Length 6 km, width of the southern portion 0.5-1.25 km, of the northern portion 1.75 km. The two portions are connected by a channel which is 1 km long and approx. 100 m wide. The surface is 5.942 km². Maximum depth is 6.4 m, average depth is 3.41 m[1]. The shores are formed by sanddunes which reach a height of 15 m, the gently sloping edge of the lake is covered with reeds and rushes. During my visit on 10 and 11 August 1928 the algal bloom was so pronounced that the net, which had a mesh width of 0.2 mm, filled up with a clump of algae the moment it was put into the water and hardly acted as a filter any more. This is perhaps also the reason why so few Bythotrephes were caught.

2. Lake Saucken. This is an unindented lake, 6 km long and 1.4 km wide. Its shores are formed by hills consisting of ground moraine, culminating in a dome 167 m high at the eastern end of the lake. On the shore of the south-eastern portion, which is the part I visited, there were pebbles and larger stones. The edge of the lake is flat, there are wide belts of (p.307 reeds in places. A profile recorded by taking soundings along a 3.4 km

---

[1] Cf. note on p. 6

long stretch resulted in two depressions being found which were up to 10 m deep. While I was there a high concentration of algal bloom prevailed.

3. Lake Usmaiten. The Hydrobiological Institute in Riga has been researching this lake for a number of years, and publications about it may be expected to appear in the near future. This large, highly indented lake with its bays and islands, its wide shorelines covered with reeds and its shallow depth can certainly be described as belonging to the eutrophic type. It contains Coregonus albula.

4. Lake Pussen. This lake, which is hardly indented, is 4.6 km long and up to 1.6 km wide. Its shores, especially those of the south-eastern portion, are formed by steeply sloping hills. The Anger stream flows through the entire lake, the southern end of which is largely covered with reeds. The bottom of the lake is reported to be very uneven, its depth is said to extend to 40 m. Coregonus albula lives in the lake.

5. Lake Wehsit. It is 7.1 km long and up to 500 m wide with rising shores and a narrow foreshore showing sparse growth of Phragmites, Sparganium, Scirpus, Nymphaea and Potamogeton. The bottom of the foreshore is sandy. At greater depth the bottom of the lake is covered with slimy, green-black mud inhabited by red Chironomus larvae. In the western and middle sections four profiles were recorded by soundings, and maximum depths of 5 m, 12.5 m, 19.5 m and 27 m were determined. Strong winds springing up on the second day of my stay prevented me from finishing my work.

Based on the above it can be said that marked eutrophication and general warming of a lake does not preclude the development of a colony of Bythotrephes in it; even under these circumstances Bythotrephes can attain a considerable

size and a high degree of fertility. This realization contradicts the assumption that Bythotrephes longimanus is a stenothermal cold water dweller and exists mainly in the deep regions of large lakes.

1.3 The relationship between Baltic Bythotrephes and Nordic Bythotrephes

Already LILLJEBORG (15), taking size as the main criterion, differentiated between two varieties of the species Bythotrephes longimanus, which he named longimana s.str. and arctica. Since among all the researchers studying Cladocera EKMAN (5) was the one most dedicated to this material, I shall now briefly put forward his views.

According to EKMAN, Bythotrephes is a cold water dweller, even if (p.308
not a pronounced one. After extensive investigation of Nordic and Central European material EKMAN reaches the conclusion that Bythotrephes found the best living conditions within a cold biotope, either in the bodies of water in the North or in the deep reaches of large lakes in temperate areas. He does not regard the North German colonies as being of equal value. He states that it has been found "only on relatively few occasions" in the Central European lowland plain despite the thorough research done in this area. Thus, according to EKMAN, the High Arctic Varietas arctica has to be seen as the true main form, and therefore longimanus, the old name of the species, has to be kept for reasons of priority.

He takes the considerable body size, the widespread distribution and the high degree of fertility of the V. arctica as proof of Bythotrephes thriving relatively better under conditions that exist at present in their most extreme form in the High North. Given a body length of 5 mm, not counting the spina, it is much larger than the southern Swedish form. EKMAN points out that

V. arctica usually produces 7-9 subitaneous eggs - I leave out the data concerning winter eggs - while at the most 4 eggs are produced in southern Sweden and Denmark.

According to EKMAN, the primitive nature of certain body features of V. arctica, when added to the characteristics of a cold-water organism, leads to enquiries into the phylogenetic background of the animal. EKMAN considers Polyphemus pediculus to be the most original form of the polyphemids, and he believes the Nordic Bythotrephes is closer to it than the Central European Bythotrephes. The comparative shortness of the 1st leg and of the spina, when compared with body length, a denser setation of the 3rd segment of the 1st leg and a darker pigmentation of the eye are thought to distinguish V. arctica from V. longimana s.str. and to contribute to its similarity with Polyphemus. EKMAN summarizes his views as follows: "The widespread distribution, the considerable size, the more numerous egg production in the North most likely mean that here the conditions of life are the most suitable for the species and correspond most closely to its organization, the reason for this being most probably that they are the closest to those surrounding the species during its phylogenetic development and on which it has concentrated its adaptability more than on any other" (p. 147).

If I attempt to review the above views of EKMAN critically, based as they are on enormous experience, I can only approach this task by pointing to the collection of my material which originates predominantly in the fauna of the eastern Baltic region and of North Germany. Unfortunately I was not in a position to extend my investigation further to include other colonies as well to any significant degree.

As my material from Lapland consisted mainly of crustaceans at the second moulting stage, I shall limit my comparisons to these. I shall start by dealing with the indications of a particularly high level of development of the species under Nordic conditions. (p.309)

The difference in size between V. arctica and longimana s.str. is quite obvious but does not seem to be as accentuated as EKMAN states. I established an average of 1516 µ for the colony of Pussen and of 2934 µ for the colony of Lapland, a difference of 1418 µ. The average for the southern Swedish colony of Värmeln was 1431 µ with a difference of 1503 µ; it was 2587 µ for the colony of Lake Constance (autumn population) with a difference of merely 347 µ. EKMAN mentions 5 mm as the body length of V. arctica, which may refer to twice moulted crustaceans; the corresponding figure given for the southern Swedish form is 2-3 mm. In this case the difference would be 3-2 mm. Incidentally, in the case of Cladocera, large body size need not point to a Nordic origin, as WAGLER once said.

I shall not venture a final judgment regarding the comparative frequency and abundance with which Bythotrephes occurs in the North and in the Baltic region. EKMAN emphasizes a general occurrence in large numbers in the North. He observed V. arctica in shallow water near the shore "often ... appearing together in enormous numbers". That much seems to be certain: the crustacean is bound to have a much wider distribution in the bodies of water in the eastern Baltic region than seemed to be the case based on the finds up to now. The number of animals encountered fluctuates widely; this was proved by vertical catches made by Prof. RIIKOJA in Lake Saadjärv where on 17 July 19.3 specimens were caught in 1 ccm of plankton, while on 1 September only 2.9 were caught. Nearly 71 crustaceans per 1 ccm of plankton were caught

in Lake Fure (Dr. OTTERSTRÖM). In addition, it is very difficult to estimate the quantitative relationship between a frankly littoral and a frankly limnetic form.

The large number of eggs produced by V. arctica (according to EKMAN usually 7-9 subitaneous eggs) is very striking and does not seem to be matched by the fertile colonies from Lake Pussen and Lake Usmaiten; there on average 6.25 and 6.44 eggs are produced. According to EKMAN, in northern Sweden (Frostviken) the main species produces up to 6 subitaneous eggs, i.e. on average fewer than the colonies in Courland and perhaps no more than the colonies of Lake Dieck. A comparison between the colonies of Lake Dieck and Lake Höft proves that geographical position is not that important as far as the number of offspring is concerned; in the case of Lake Dieck, the average (number of offspring) at the third stage was 5.39, while in the case of Lake Höft is was only 2.96. The figures I am quoting are taken from statistical series and cannot therefore be compared too closely with the older data.

I shall now move on to discuss the evidence for the primitive nature (p.310) of the body features.

I cannot say anything concerning the spine; in specimens of V. arctica sent to me it was often impossible to measure it exactly because of minor injuries. As far as the relative length of the 1st leg is concerned, EKMAN writes: "In the case of the northern forms, the length of the three distal segments of the above-mentioned pair of legs excluding the terminal setae in different colonies was on average 42.2-62.4% of body length measured from the frons to the anus; in the case of the southern forms, however, the corresponding figure is much higher, namely 88.2%. For the colony in Lapland the relative length I found was 88.2%, and I was unable to discover a difference between

this average and the averages for the colonies of Lake Värmeln, Lake Fure and Lake Saadjärv. In the colony of Lake Dieck the percentage was smallest at 81.0%; the highest percentages were found in the colonies of Lake Pussen at 94.0% and Lake Constance at 118.1%. - As far as the number of setae covering the 3rd segment of the 1st leg is concerned, arctica with an average count of 10.24 tops all the other colonies. Next is the colony of Lake Constance with an average count of 7.87 and that of Lake Saadjärv with an average count of 7.82. - I agree with EKMAN about the pigmentation of the eye: I investigated the eyes of specimens from Lake Dieck, Lake Selenter and Lake Pussen, and in none of them did I find conditions similar to those mentioned by him in the case of V. arctica, because the pigment was always limited to the retinular cells and the inner parts of the supporting cells (cf. Fig. 20).

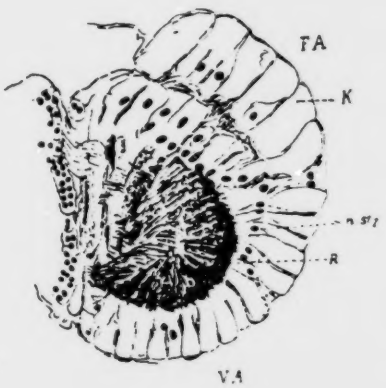

Fig. 20. Eye of a specimen from the colony of Lake Selent. The section did not turn out to be precisely sagittal. Pigmentation is strictly limited to the retinular cells and the inner parts of the supporting cells (Obj. 7). FA anterior eye, VA ventral eye, K crystal cone, R retina, n stz nuclei of the supporting cells.

To summarize the foregoing: V. arctica differs from V. longimana (p.311) by its size (according to EKMAN), by the relative shortness of its spina, the

denser setation of the 3rd segment of the 1st leg and the heavier pigmentation of the eye. According to my measurements there is no difference in the relative length of the 1st leg, nothing conclusive can be said about frequency and abundance, and the difference in fertility seems less pronounced than one thought one had to assume on the basis of older data.

The question must now be asked to what extent the differences which have been discovered are based on geographical and phyletic reasons or are dependent on ecological conditions. This dependence was certainly considered by EKMAN.

Bythotrephes of Central Europe is clearly a limnetic cladoceran; this is not altered by the fact that occasionally it has been found in small and shallow bodies of water. According to EKMAN both forms of Bythotrephes long. occurred in the shallow as well as the deep bodies of water of the birch region and of the grey willow region and also in the smallest and warmest bodies of water of the lichen region. In all cases B. long. v. arctica was restricted to the littoral zone, while v. longimana s.str. occurred in both the pelagic and littoral zones in the bodies of water of the birch region and the grey willow region, and only in the pelagic zone in the small bodies of water of the lichen region. Neither form occurs in the larger lakes of the lichen region. It follows from these data that v. arctica is tied to a littoral form of existence, while longimana s.str. is tied more, though not exclusively, to a pelagic existence. EKMAN says about v. arctica: "I would therefore assume that the former is always a littoral form."

If we leave aside setation, since we know nothing about its significance, we are struck by the fact that the differences mentioned could indeed be connected with the habitat, something that EKMAN himself hints at. Smaller body

size in the Central European form need not be a result of inferior living conditions but can be seen as adaptation to the limnetic way of life. WOLTERECK (28) says (p. 41) "... all of the Cladocera have become small ... some of the pelagic species became even smaller, because this is again required by the surroundings" (facilitating floating, staying suspended, perhaps also a greater degree of protection from swarms of young fish, etc.).

The fact that arctica is larger than longimana ties in well with other comparative observations. HESSE (9) writes (p. 164): "The temperature of (p.312) sea water exerts a peculiar influence on the size of animals. That is to say, it has become evident that cold-water animals, namely the forms found in polar seas and deep sea regions, frequently reach dimensions that distinguish them in comparison to their relatives. This is valid to the point that within the same species the specimens found in cold water are on average larger than those from warmer parts of the sea ..."

WAGLER (25), too, makes a statement regarding this question (p. 295): "The arctic specimens of the species Holopedium gibberum, Bythotrephes longimanus, Polyphemus pediculus and Leptodora Kindtii are always larger than the specimens taken from our bodies of water". WAGLER refuses to infer arctic origin from size.

We are dealing here with, by and large, a general rule and will have to admit that WAGLER is right.

It is doubtful whether a relatively longer spina can be explained along the lines of the suspended swimming habit hypothesized by OSTWALD and WESENBERG-LUND. According to WOLTERECK (28), the highly specialized task of the spina is that of a steering mechanism and a "towing process" (p. 35); according to

WESENBERG-LUND (29), it is a balance organ which makes possible horizontal motion, and it is questionable whether in addition it can serve to enlarge the cross-section of the body. As a result of my measurements we know that the spine is, relatively speaking, longest in the case of the youngest animals; it is, relatively speaking, shortest in the case of those that have moulted twice and are naturally the heaviest, which would militate against the suspended swimming hypothesis. - The greater transparency of the body is characteristic of lake dwellers. The darker pigmentation of the eyes in the case of the littoral form might be explained by the necessity of increased protection from light. It is striking, however, to observe, as EKMAN did, that B. cederströmii living under similar conditions does not show increased pigmentation.

If we take the point of view, as many researchers do, that the limnetic Cladocera descended from the littoral Cladocera (HESSE (9), p. 346, WESENBERG-LUND (29), p. 12), we shall not make an exception in the case of Bythotrephes. We could thus share EKMAN's view that v. arctica is the more primitive and v. longimana s.str. the less primitive form. This assumption is based on the premise that the ancestors of the recent v. arctica were also littoral rather than, perhaps, having lived a limnetic life. However, it is quite possible to assume the opposite and regard arctica as the littoral deviation of an older limnetic species. However complicated such a hypothesis may sound, it might be solidly founded as soon as the development of the cyclopean eye can be explained merely as a deep sea formation. MILTZ (18) is of this opinion when he writes: "There is no doubt that the polyphemids represent a more recent form of Cladocera; these were forced by circumstances to assume a predatory existence. This transformation happened perhaps in a mountain lake of considerable depth which also had few plants." And again: "The data contained in the above concerning the structure of the eye in the various genera of polyphemid fully confirm the

(p.313

view brought forward by CHUN that in the case of Cladocera the eye of some representatives of this group evolved in the course of time in a manner similar in principle to the changes detected in the case of deep sea crustaceans (p. 53 and p. 27). If these procouncements are correct, they could also be applied to the eye of v. arctica. EKMAN for his part considers the predatory nature of the Bythotrephes-like crustaceans sufficient to explain the transformation even without taking their pelagic existence into account. He also stresses that the retinopigmentary eye of the Bythotrephes is not built according to the same principle as the iridopigmentary eye of the true deep sea forms. However, CHUN says (quoted after MILTZ, p. 7): "As a result of more extensive adaptation to life in darkness, a lack of pigment becomes apparent, because either the pigment of the iris (retinopigmentary eyes) or the pigment of the retina (iridopigmentary eyes) decreases. - Prof. FRANZ advised me in a letter that the polyphemids are the only genus containing many frequent species that are sea-dwellers and that they therefore are more likely than other Cladocera to have originated in the sea and to have been pelagic. - I leave it open which of the two views I consider to be correct.

To summarize briefly: EKMAN's hypothesis culminates in the assumption that v. arctica is closest to the original type of the species, while LILLJEBORG's longimana s.str. is a more or less stunted subsidiary form adapted to the limnetic way of life.

The wide distribution and obvious flourishing of colonies of Bythotrephes in the eastern Baltic region is evidence that this race is not inferior to the Nordic colonies and makes us regard both as being of equal value. We can thus disregard the special importance of Nordic conditions of life for the flourishing of any species and immediately address the question of which

differences are due to ecological reasons and which can be seen as phylogenetic reminiscences. We saw that most of the body features by which longimana s.str. and v. arctica differ might be explained as an adaptation to the limnetic way of life, with really only one exception, namely the (p.314) sparser setation of the 5th segment of the 1st leg. If arctica is more similar to Polyphemus pediculus than to longimana s.str. regarding this specific feature, special family relationships might be involved. Other corresponding features might also count as parallel adaptations to the littoral environment.

I would therefore like to stress the ecological element of the matter whenever arctica and longimana s.str. are being compared. The former is a stenothermal cold water animal with a littoral way of life while the latter is eurythermal and has a pronounced limnetic way of life. This does not yet provide an explanation for any phylogenetic connection.

I cannot refute EKMAN's hypothesis by means of the factual material available to me; these facts, however, show that a deviating point of view might be possible.

At this point a major problem arises out of certain observations by LILLJEBORG and EKMAN. Both researchers have discovered transitions between the Nordic and the southern Swedish forms. EKMAN writes: "...v. arctica gradually changes into the main form, regarding both size and the other characteristics." LILLJEBORG mentions transitional forms between the two, and the material collected by me forms a continuous transitional series. LILLJEBORG says of v. arctica: "The second form seems to reach its maximum in the northernmost parts of Scandinavia. It seems to be smaller further south; I for example have caught specimens around Östersund in Jämtland which are only 3mm long

but which, incidentally, correspond to the larger forms except for the terminal stalk. I know of one form from Lake Womb in Schonen province which comes very close to the specimens from Jämtland, whose body measures 2.7 mm and whose terminal stalk is 6 mm long ..." (p. 616).

I am unable to judge for myself to what extent the transitional forms mentioned here might belong to arctica or longimana s.str. My investigation involving Bosmina have made me realize, however, that delineating similar and widely varying forms such as the Cladocera is only possible with the aid of statistics of variation; my work relating to the Baltic colonies of Bythotrephes has only strengthened this belief. Furthermore, I would like to stress here once more that a comparison should only be made between animals at the same moulting stage. I would therefore consider it entirely appropriate to carry out this kind of investigation on the Nordic colonies as well.

14. The colonization of Central Europe (p.315)

There is no question that the ice age played a decisive role in the spreading of Bythotrephes, and the Baltic glaciation is the period that is relevant for the area we are interested in. Frequently Bythotrephes is regarded as a relict from the ice age.

We owe EKMAN (6) what is probably the most thorough work on the related terminology.

He believes that three conditions have to be met in order to be allowed to call a species or a certain stock (colony) of a species a relict from the ice age: "1. The species has to be a stenothermal cold-water dweller. 2. The distribution, or rather, the distribution ecology, must show that the capacity for active migration or for being spread is so small that the species

cannot be considered a stenothermal cold-water cosmopolitan species. 3. The stock in question has to have been left behind at the same place where it now exists, from a period of glacial conditions. Otherwise it can at best be considered a pseudo-relict" (p. 28). We can see that after the first two points the cold-water stenothermy is decisive. As was demonstrated in the previous section, Bythotrephes long. is by no means a stenothermal cold-water dweller. The requirement of the third point is therefore now not being met either.

Out of the find spots discovered up to now in the eastern Baltic region, three (Lake Saucken, Lake Wehsit and Lake Saadjärv) are situated quite far inland in a ground-moraine landscape, while three (Lake Usmaiten, Lake Pussen and Lake Duhnje-Lihlast) are situated close to the seashore. As the eastern Baltic coastal plain has been subject to transgressions several times during the Holocene, the regions containing these latter lakes were at times submerged. The lakes therefore did not come into being until some time of indeterminate length after the ice had retreated, and this is the earliest that their colonization could begin.

Lake Pussen and Lake Usmaiten are without any doubt older than Lake Duhnje-Lihlast. According to a letter from Prof. KRAUS (Riga) for which I am most grateful, Lake Pussen and Lake Usmaiten belong to an ancient subsidence basin: they probably were haffs at some stage and were connected then with the Ancylus Lake before becoming inland lakes. Lake Duhnje-Lihlast is now situated close to the sea, separated from it only by a chain of dunes. According to KRAUS, this double lake is a recent haff-like body of water cut off from the bight and was formerly connected with the Littorina Sea. The colonies of Bythotrephes cannot have arrived in these lakes until a more recent period of the Holocene. By contrast, the colonies of Lake Saadjärv, Lake Saucken and (p.316) Lake Wehsit might have taken up their present habitat immediately after the

retreat of the ice. But even they cannot be referred to as relicts from the ice age, because they do not meet EKMAN's first requirement.

It remains completely uncertain how the three first-named lakes were colonized. Immigration from the sea is conceivable. LILLJEBORG (15) found "a slightly smaller form in the sea in Skälderviken Bay near the Kullaberg Mountains at a depth of approx. 15 fathoms" and assumes that it was brought there by the River Rönne from Lake Ring (p. 616). Such migration does happen, even over long distances, as evidenced by the occurrence of Bythotrephes cederströmii in the southern reaches of the Volga River (24). Whatever the case may be, we may assume that the animals discovered in the Kattegat are members of a colony that is established in the sea and thrives in salt water. It is then perfectly possible that under certain circumstances re-immigration into a haff, later to become an inland lake, has taken place. On the other hand, a process of dispersal of the animal from land to sea, either through connecting water bodies or through aquatic birds, can also not be ruled out. However, we are dealing here with speculation lacking any factual foundation.

The remarkable adaptability of Bythotrephes to the size and depth of water bodies, its tolerance towards temperature changes, oxygen and salt content make it appear feasible that it was widespread in Central Europe even before the start of the ice age rather than arriving there from the North during the ice age. After the ice had covered the area around the Baltic Sea, it survived in an ice-free region, only to re-settle in its old habitat after the ice had retreated. The littoral stenothermal form and the limnetic eurythermal form inhabited adjoining zones without any intermixing taking place. The former has always been subarctic. The reason why Bythotrephes is not found in mountain lakes in the Alps is the inability of the subarctic form to cross the

temperate foothills and the fact that the limnetic form did not follow the retreating Alpine glaciers any further than was appropriate to its organization.

15. The systematics of Bythotrephes longimanus

In his classic work on the Cladocera of Sweden, LILLJEBORG divided the species longimanus into three varieties: the main form v. longimana, the Nordic form v. arctica and a third form, v. brevimana. (p.317)

As we realized on p. 279, animals possessing a relatively short 5th segment of the 1st leg occur in varying numbers in most of the colonies. The colony in Lake Constance, of which the 2nd stage was investigated is the only one where all animals belong to the longimanus form. In the case of the other colonies, the number of brevimanus animals fluctuates between 2.1% (Lake Pussen) and 83.6% (Lake Dieck) of all animals in the 3rd stage and between 7.7% (Lapland) and 100% (Lake Dieck) of all animals in the 2nd stage. A second rule emerged, namely that there is an increase, in per cent, of longimanus animals with each successive moulting. As the brevimanus animals do not differ in any other way from the other form, separating it off into a variety by itself is not possible.

LILLJEBORG's v. arctica belongs to the North of Europe. The evaluation of this variety by EKMAN has already been dealt with on p. 11. It has quite rightly been separated from the other form.

V. longimana s.str. comprises mainly the colonies of southern Sweden, of Denmark and of the sub-alpine lakes. It goes without saying that the North German finds were counted among these, too.

Although the material I worked with is far from complete, I shall attempt to organize the species longimanus. This attempt will not be in any way definitive. Only further investigation will show how much may have to be added or altered. The terminology used has been taken from the work of SEMENOVTIAN-SHANSKY (21). I was more concerned with relative similarities than with a definitive determination within the system.

The wide range of variations of the investigated forms makes the delineation of the systematic units extremely difficult. As the averages calculated statistically are not in themselves sufficient to establish greater or lesser agreement within the groups of characteristics, I used a method which KOSMINSKI (13) used in his investigations of the cyclopids. KOSMINSKI calculated the range of varietion of certain characteristics of the units to be compared according to the formula $M \pm \sigma$ and $M \pm 2\sigma$. $M_1 + \sigma_1$ $M_2 - \sigma_2$ denotes an antagonistic relationship, $M_1 + 2\sigma_1$ $M_2 - 2\sigma_2$ denotes a hyperantagonistic relationship between the two forms to be compared. Of course in the latter case a greater systematic variety exists than in the former.

I am now going to tabulate the characteristics in respect of which the colonies that are being compared acted hyperantagonistically or antagonistically . The comparison of the Baltic colonies with those from Lake Constance and from Lapland was made on the basis of the 2nd moulting stage, the (p.318) comparison of the Baltic colonies among themselves was based on the 3rd moulting stage. Of all the characteristics only body length, number of setae, indices for the spina, the 1st leg, the antenna stalk and the 5th segment of the 1st leg were taken into account.

Table 21.

Hyperantagonism at the 2nd moulting stage

(Hyperantagonism did not exist in the case of the relative lengths of the spina, of the 1st leg and of the antenna).

	(4) Pussen	(4) Saadjärv	(4) Dieckisee	(4) Furesee	(4) Värmeln	(5) Bodensee	(6) Lappmark
	(7)						
(1) Körperlänge	Bd. Lpm.	Bd. Lpm.	Bd. Lpm.	Bd. Lpm.	Bd. Lpm.	Pus. Sdj. Dk. Fur. Vrm.	Pus. Sdj. Dk. Fur. Vrm.
(2) Borstenzahl	Lpm.	Lpm.	Lpm.	Lpm.	Lpm.	—	Pus. Sdj. Dk. Fur. Vrm.
(3) relat. Länge d. 5. Gliedes	—	Bd.	Bd-Lpm.	Bd.	Bd.	Sdj. Dk. Fur. Vrm. Lpm.	Bd.

Translation key:

1. length of body
2. number of setae
3. relative length of 5th segment
4. names of lakes
5. Lake Constance
6. Lapland
7. abbreviated names of lakes

We gather from the Table that

1. the Baltic colonies (Lake Pussen, Lake Saadjärv, Lake Dieck, Lake Fure and Lake Värmeln) do not behave hyperantagonistically among themselves;

2. that by contrast a hyperantagonistic relationship exists between the Baltic colonies and those of Lake Constance and from Lapland; the differences involved are body length between the Baltic colony and each of the other two, the number of setae covering the 5th segment of the 1st leg, as far as the colony in Lapland is concerned, and the relative length of the 5th segment of the 1st leg as far as the colony from Lake Constance is concerned (and in the case of the colony from Lake Dieck, also as far as the colony from Lapland is concerned).

3. Between the colonies from Lake Constance and those from Lapland a hyperantagonistic relationship exists only as far as the relative length of the 5th segment of the 1st leg is concerned.

From this follows:

4. The relationships of the Baltic colonies to the other two correspond to those listed under 2. In addition, there is antagonism of all Baltic colonies towards the colony from Lake Constance as far as the relative length of the 1st leg is concerned (in the case of Lake Pussen, also as far as the length of the 5th segment is concerned) and antagonism of all the Baltic colonies (except for that of Lake Pussen) towards that of Lapland as far as the relative length of the 5th segment is concerned. And finally, there is an antagonistic contrast between the colonies of Lake Saadjärv, Lake Dieck and Lake Värmeln on the one hand and that of Lapland on the other, as far as the relative length of the antenna is concerned.

Table 22. (p.319)

Antagonism at the 2nd moulting stage

(no antagonism in the case of relative length of spina).

	(6) Pussen	(6) Saadjärv	(6) Dicksee	(6) Fürsee	(6) Värmeln	(7) Bodensee	(8) Lappmark
(1) Körperlänge	Bd. Lpm. Dk.	Bd. Lpm.	Pus. Fur. Vrm. Bd. Lpm.	Bd. Lpm. Dk.	Bd. Lpm. Dk.	Pus. Sdj. Fur. Dk. Vrm.	Pus. Sdj. Dk. Fur. Vrm.
(2) Borstenzahl	Lpm.	Lpm Dk.	Sdj. Bd. Lpm	Lpm.	Lpm.	Lpm. Dk.	Pus. Sdj. Dk. Fur. Vrm. Bd.
(3) rel. Länge d. 1. Beins	Bd.	Bd.	Bd	Bd.	Bd.	Pus. Sdj. Dk. Fur. Vrm. Lpm.	Bd.
(4) rel. Länge d. Antenne	—	Lpm.	Lpm.	—	Lpm.	—	Sdj. Dk. Vrm.
(5) rel. Länge d. 5. Gl. d. 1. Beins	Bd. Dk.	Bd. Lpm.	Pus. Fur. Bd. Lpm.	Dk. Bd. Lpm.	Bd. Lpm.	Pus. Sdj. Dk. Fur. Vrm. Lpm.	Sdj. Dk. Fur. Vrm. Bd.

(Translation key on next page)

Translation key (of Table 22)

1. length of body
2. number of setae
3. relative length of 1st leg
4. relative length of antenna
5. relative length of 5th segment of 1st leg
6. names of lakes
7. Lake Constance
8. Lapland
9. abbreviated names of lakes

5. The colonies of Lake Pussen, Lake Saadjärv, Lake Fure and Lake Värmeln form a uniform group (without antagonistic characteristics). However, between them and the colony of Lake Dieck there exists multiple antagonism, for example relating to body size, setation and relative length of the 5th segment.

6. There is antagonism between the colonies from Lake Constance and those from Lapland as far as setation and relative length of the 1st leg and its 5th segment are concerned.

No hyperantagonistic characteristics existed between the Baltic colonies (3rd stage of moulting). Table 23 informs about antagonistic characteristics.

Table 23.

Antagonism at the 3rd moulting stage

(no antagonism in the case of length of 1st leg or of length of antenna stalk)

	(5) Pussen	(5) Usmalten	(5) Saadjärv	(5) Dieckscc	(5) Höftsee	(5) Soldiner See	(5) Furesee	(5) Värmeln
(1) Körperlänge	(6) Dk. Hft.	Fur.	Dk. Hft.	Pus. Sdj. Fur. Vrm.	Pus. Sdj. Fur. Vrm.	Fur.	Usm. Dk. Sld. Hft.	Dk. Sld. Hft.
(2) Borstenzahl	—	—	Dk. Sld.	Sdj.	—	Sdj.	—	—
(3) rel. Länge d. Spina	—	—	Vrm.	—	—	—	—	Sdj.
(4) rel. Länge d. 5.Gl. d. 1. B.	Sdj. Dk. Fur.	—	Pus.	Pus.	—	—	Pus.	—

(Translation key on next page)

Translation key (of Table 23)

1. length of body
2. number of setae
3. relative length of the spina
4. relative length of the 5th segment of the 1st leg
5. names of lakes
6. abbreviated names of lakes

7. Only one case of antagonism exists beween the eastern Baltic colonies (Lake Pussen, Lake Usmaiten, Lake Saadjärv) (between Lake Pussen and Lake Saadjärv regarding the relative length of the 5th segment).

8. No antagonism exists between the North German colonies (Lake Dieck, Lake Höft, Lake Soldin), but there are 7 cases of antagonism between these (p.320) and the colonies just mentioned.

9. No antagonism exists between the colony of Lake Fure and that of Lake Värmeln; however, there are 3 instances of antagonism between these on the one hand and the eastern Baltic colonies on the other, and 6 cases between these and the North German ones.

10. The antagonistic characteristics relate mostly to body length, and the eastern Baltic colonies and the Scandinavian colonies, which are uniform among themselves, are contrasted with the North German ones. The colonies from Lake Usmaiten and Lake Soldin take up a position in-between these contrasting ones. The colony of Lake Pussen contrasts with the colonies of Saadjärv, Lake Dieck and Lake Fure regarding the relative length of the 5th segment, the colony of Lake Saadjärv contrasts with the colonies of Lake Dieck and Lake Soldin with regard to setation, and also contrasts with the colony of Lake Värmeln regarding the relative length of the spina.

We shall summarize the results of this comparison by stating first of all that considerable differences exist between the Baltic colonies and those from

Lake Constance and from Lapland; between the latter two there are greater differences than exist between the individual Baltic colonies. We thus divide Bythotrephes longimanus into three subdivisions which we shall name arcticus, balticus and brigantinus (after Lake Constance). For the time being their systematic value cannot be determined with any certainty, because questions regarding transitional forms and geographic delineation have to be clarified. In any case, they should at the very least be subspecies or races. EKMAN also writes regarding the Swiss colonies that it seems "as if this might be the emergence of a new species". According to the trinominal terminology the name denoting the subspecies should be added to the names of the genus and the species, i.e. B. long. balticus, arcticus and brigantinus.

The differences between the individual Baltic colonies are considerably smaller, but the eastern Baltic ones show more similarities among themselves than they do compared with the North German colonies, and vice-versa. The two Scandinavian colonies are more loosely linked, but both more closely resemble the eastern Baltic ones than they do the North German ones.

SEMENOV-TIAN-SHANSKY calls "particularly small, local-geographic units" 'nations' (nationes) and in such cases puts an (n) after the name of the subspecies, together with the appropriate designation.

We can proceed here in the same way and first distinguish between a North German, a Scandinavian and an eastern Baltic 'nation'. As the first one of these inhabits primarily the lakes of the Prussian state, I suggest for it the designation borussica. As long as no drastic difference can be found (p.321) between Danish and Swedish colonies, they could be grouped together under the name scandinavica. According to the samples taken, the eastern Baltic 'nation' should comprise all the colonies in Estonia, Livonia and Courland. These

regions shared the name Livonia after their first appearance in Central European history, so the 'nation' could be named livonica.

The (preliminary) system would look like this:

1. Bythotrephes longimanus balticus n. scandinavica
   n. borussica
   n. livonica
2. " " arcticus
3. " " brigantinus

The type and formation of the distinctive body characteristics and the conditions of fertility are dealt with on p. 284 and p. 293. Table 24 is an attempt to identify the colonies according to the size of their most distinctive characteristics. Unfortunately it was not possible to achieve a satisfactory result by using figures arrived at through calculation, therefore the subjective method of estimating had to be resorted to frequently.

Table 24

Body characteristics according to size

kl = small m = medium gr = large s gr = very large

	Pus	Usm	Sdj	Dk	Hft	Sld	Fur	Vrm	Bd	Lpm
Länge des Körpers . .	m	m	m	kl	kl	kl	m	m	gr	s gr
rel. Länge d. Spina . .	m	m	m	m	m	m	m	gr	kl	–
rel. Länge d. 1. Beines	m	m	kl	kl	m	kl	kl	kl	s gr	kl
rel. Länge d. 5. Gliedes d. 1. Beines	gr	gr	kl	kl	gr	gr	m	kl	s gr	gr
rel. Länge d. Antennenstiels	m	m	m	gr	gr	–	kl	m	kl	kl
Borstenzahl	gr	m	gr	kl	m	kl	m	m	gr	s gr

(Translation key on next page)

Translation key (of Table 24)

1. length of body
2. relative length of spina
3. relative length of 1st leg
4. realtive length of 5th segment of 1st leg
5. relative length of antenna stalk
6. number of setae
7. abbreviated names of lakes
8. Lake Constance
9. Lapland

Only a few characteristics are sufficiently pronounced to be used for identification purposes. Among those are the considerable body length and large number of setae in the case of longimanus arcticus, and in the case of long. brigantinus the extremely high index for the 5th segment of the 1st leg as well as the small size of seta No. 2 on the 3rd segment. Having said this, longimanus balticus is easy to delineate from the other two. No such pro- (p.322) nounced characteristics exist to distinguish the Baltic 'nations' from one another; there are only more or less unstable groups of characteristics of changing composition and intensity. With our present knowledge, which is based on the summer population of a few colonies, no reliable delineation is possible. Nevertheless, some striking features stand out. Livonica is relatively large, borussica is small. The colony of Lake Värmeln has a remarkably high spine length index. The antenna length index is very high in the case of borussica, ect.

Given the great similarity and range of variation of these closely related forms, it would nevertheless still not be possible to determine the appropriate group into which a given animal would fit, on the basis of the characteristics investigated to date. Despite this imperfection, we can affirm the factual diversity of the 'nations', because very small "hereditary local races" have been proved to exist in the case of other Cladocera (WOLTERBECK, 28).

16. Some closing remarks

1. An exact determination of the morphological features of Bythotrephes longimanus, Bosmina, Daphnia and other Cladocera is only possible through the calculation of averages and of several other identifying characteristics using statistics of variation.

2. When conducting comparative investigations, the various moulting stages have to be kept strictly separate.

3. Each two homologous appendages on the left-hand and right-hand side are asymmetrical, which is of no practical consequence.

4. Length of body on the one hand and length of the spina and of the 1st leg on the other exhibit a positive correlation. The same is true in the case of the 3rd and 5th segments of the 1st leg.

5. The body characteristics of the colonies exhibit such far-reaching differences that the colonies can be divided into separate groups on the basis of averages.

6. The brevimanus form occurs in almost all the colonies but does so in varying numbers. It occurs most frequently at the first stage of moulting and its incidence diminishes with each successive stage.

7. The embryos develop independent of the mother's moulting stage.

8. The average number of offspring is smaller for primagravidae than for multigravidae.

9. Males are distinguished from females by a shorter 1st leg, especially its 4th segment.

10. Bythotrephes longimanus occurs not only in deep lakes but also in shallow ponds with high water temperature and low oxygen content.

11. LILLJEBORG's Bythotrephes longimanus s.str. and arcticus are forms of equal value; the former is eurythermal and limnetic, the latter is psychro-stenothermal and littoral.

12. Bythotrephes longimanus is not a relict from the ice age. It colonized some of the Baltic lakes only in the most recent diluvial past.

13. We are subdividing (provisionally) the species longimanus into three subspecies: balticus, arcticus and brigantinus. Within the Baltic subspecies three geographically limited 'nations' (nationes), scandinavica, borussica and livonica can be distinguished.

17. Bibliography

1. Behning, Studien über vergleichende Morphologie der Phyllopodenextremitäten. Leipzig 1912.
2. Claus, Zur Kenntnis des Baues und der Organisation der Polyphemiden. Wien 1877.
3. Duncker, Symmetrie und Asymmetrie bei bilat. Tieren. Arch. f. Entw. mech. Bd. 17. 1904.
4. — Über einige Lokalformen von *Pleuronectes platessa*. Mitt. a. d. Nat. Mus. Hamburg 1913.
5. Ekman, Die Phyllopoden, Cladoceren und Copepoden der nordschwedischen Hochgebirge. Zool. Jahrb. 1904.
6. — Vorschläge und Erörterungen zur Reliktenfrage. Arch. f. Zool. Bd. 9. Nr. 17. 1915.
7. Freidenfelt, Zur Frage der Berechtigung relativer Maßangaben in der Cladocerenforschung. Rev. d. Hydrobiol. 9.
8. Friederichsen, Method. Atlas zur Länderkunde von Europa. Lief. I. 1914.
9. Hesse, Tiergeographie auf ökologischer Grundlage. Jena 1924.
10. Ischreyt, *Bosmina coregoni* in Kurland. Arch. f. Hydrob. 18.
11. — Ein weiterer Beitrag zur Bosminenfauna Kurlands. Arch. f. Hydrob. 19.
12. Keilhack und Rühe, Über das Vorkommen der *Bythotrephes longimanus* in Norddeutschland. Rev. d. ges. Hydrob. 3. 1910.
13. Kozminski, Über die Variabilität der Cyclopiden. Bull. intern. de l'academie Polon. d. sc. et d. let. 1927.
14. Kuptsch, Die Cladoceren der Umgegend Rigas. Arch. f. Hydrob. 18.
15. Lilljeborg, Cladocera Sueciae. Upsala 1900.
16. Ludwig, Die Küstenseen des Rigaer Meerbusens. Riga 1908.
17. Meyer und Baumann, Beiträge zur Klimakunde des ostbaltischen Gebietes. Korr. d. Naturf. Ver. Riga 1927.
18. Miltz, Das Auge der Polyphemiden. Zool. Heft 28. 1899.
19. Rammner, Über die postembryonale Entwicklung der Clad. Scaphol. mucr. Arch. f. Entwickl. mech. Bd. 113. 1928.
20. — Über periodische Erscheinungen am Cladoceren-Individuum. Int. Rev. f. Hydrob. Bd. 21. 1929.
21. Semenov-Tian-Shansky, Die taxonischen Grenzen der Art und ihrer Unterabteilung. Berlin 1910.
22. Storch, Cladocera. Aus Biologie der Tiere Deutschlands. 15. 1925.
23. Thienemann, Temperatur und Sauerstoffverhältnisse eisbedeckter Seen des Plöner Gebiets. Arch. f. Hydrob. 18.
24. Tschugunoff, Über *Byth. cederstr.* aus der unteren Wolga. Russ. Hydrob. Zeitschr. I. 1922.
25. Wagler, Über das System, die geographische Verbreitung der *Daphn. cucullata*. Int. Rev. d. Hydrob. 1923.
26. — Branchiopoda, Phyllopoda. Aus Handb. d. Zool. 1927.
27. Weismann, Beiträge zur Naturgeschichte der Daphnoiden. Leipzig 1876—1879.
28. Woltereck, Variation und Artbildung. Int. Rev. d. Hydrob. 11. 1923.
29. Wesenberg-Lund, Grundzüge der Biologie und Geographie der Süßwasserplanktons. Int. Rev. d. Hydrob. 1910.
30. Zschokke, Die Beziehungen der mitteleuropäischen Tierwelt zur Eiszeit. Verh. d. D. Zool. Ges. 1908.

1. Studies in comparative morphology of the extremities of phyllopods
2. Information on the structure and organization of the polyphemids
3. Symmetry and asymmetry in bilateral animals
4. Some local forms of Pleurenectes platessa
5. The Phyllopoda, Cladocera and Copepoda of the high mountains of northern Sweden
6. Suggestions and discussions regarding the question of relicts
7. On the justification for using relative measurements in the research into Cladocera
8. Systematic atlas of the geography of Europe
9. Ecologically based zoo geography
10. Bosmina coregoni in Courland
11. Further contribution to the Bosmina fauna of Courland
12. The occurrence of Bythotrephes longimanus in North Germany
13. On the variability of the cyclopids
14. The Cladocera of the surroundings of Riga
16. The Coastal lakes of the Bight of Riga
17. Contributions to the climatology of the eastern Baltic region
18. The eyes of polyphemids
19. The post-embryonic development of Clad. Scaphol. mucr.
20. Periodic phenomena exhibited by Cladocera
21. The taxonic limits of the species and its subdivision
22. From Biology of the fauna of Germany

23. Temperature and oxygen conditions in ice-covered lakes of the region of Plön

24. Byth. cederstr. occurring in the lower Volga River

25. On the system and geographical distribution of Daphn. cucullata

27. Contributions to the natural history of the daphnoids

28. Variation and formation of species

29. Fundamentals of biology and geography of fresh-water plankton

30. The relationship of the Central European fauna to the ice age